Expanding the pulse-reserve paradigm to microorganisms on the basis of differential reserve management strategies

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Abstract (150 words)

The pulse-reserve paradigm (PRP) is central in dryland ecology, although traits of microorganisms were not explicitly considered in its inception. We asked if the PRP could be reframed to encompass organisms both large and small. We used a synthetic review of recent advances in arid land microbial autoecology combined with a mathematically explicit theoretical model. Preserving the PRPs original core of adaptations by reserve building, the model considers differential organismal strategies to manage these reserves. It proposes a gradient of organisms according to their reserve strategies, from nimble responders (NIRs) to torpid responders (TORs). It predicts how organismal fitness depends on pulse regimes and reserve strategies thus explaining organismal diversification and distribution. After accounting for scaling phenomena and redefining the microscale meaning of aridity, it becomes patent that the PRP is applicable to microbes, and that this modified PRP represents an inclusive theoretical framework working across life-forms.

Keywords: microbes, plants, aridlands, adaptations, theoretical ecology

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Drylands, which encompass deserts, shrublands, grasslands and savannas, account for 40% of the terrestrial surface (Průhová, 2016), 30% of global carbon fixation (Field *et al.*, 1998) and explain most of the interannual variability of the global carbon cycle (Poulter *et al.*, 2014). In addition, drylands are home of 30% of the human population and to some of most vulnerable groups of people, who are often immediately dependent on resources from the natural environment (Reynolds *et al.*, 2007). However, theoretical frameworks of dryland functioning are scarce. This is particularly relevant when inclusive management of multiple ecosystem services is desired (Yahdjian *et al.*, 2015, Hoover *et al.*, 2020), including conservation of biological diversity as one such desired service. For example, to inform Managed Relocation efforts in the face of global climate change (Richardson *et al.*, 2009), it would be relevant to have theoretical underpinnings of general applicability at the organism level. Additionally, microbial physiology, if not microbially-mediated processes, is underrepresented from the formulation of dryland ecological theory. A reasonable way to remedy this situation is to evaluate if current plant-based theoretical frameworks would accommodate the inclusion of microbes. The pulse-reserve paradigm (PRP) constitutes arguably the most important and enduring paradigm in dryland ecology since its postulation by Noy-Meir (Noy-Meir, 1973) almost 50 years ago. It holds that dryland ecosystems undergo cyclical dynamics in which rare rainfall events trigger a flow of resources, mostly carbohydrates and nutrients from reserves (seeds or perennial plant organs) to an existing plant. During the pulse, the plant grows new leaves and roots devoting most of the acquired resources through photosynthesis and absorption from the soil to new growth. Next, the plant starts sending resources to reserve organs that are replenished towards the end of this pulse to prepare for dormancy between pulses. As a new cycle starts with the next pulse, a new flow from reserves to growth will be triggered. The PRP was largely based on keen observations of the climatic rigors typical of drylands and on insightful naturalistic observations of plant life strategies and it has been subject to subsequent refinements and derivations relating to specific aspects like the importance of response thresholds (Schwinning *et al.*, 2004), functional plant types (Ogle & Reynolds, 2004), and interactions with nutrient pulses (Collins *et al.*, 2014). It remains one of the most cited works in the field, though microbes and microbial processes were under-represented at inception. It is “plant-centric” (Collins *et al.*, 2014). And yet, the roles that microbes and their assemblages (microbiomes) play in dryland ecology have become ever more patent during the last decades (Bashan & de-Bashan, 2010). Not only are

microbes influential as agents of disease, for which there is a long history of recognition, but they are now understood to be ubiquitous, sometimes intricately integrated partners in mutualisms with both plants and animals. They are also responsible for much of the biogeochemical cycling, and, in the face of limits to plant cover and productivity imposed by aridity, they can take on some basic ecosystem processes such as primary productivity and soil stabilization. Logically, efforts to bring microbial processes into the fold of the PRP eventually followed (Collins *et al.*, 2008, Collins *et al.*, 2014, Šťovíček *et al.*, 2017). As so much in microbial ecology, however, these contributions were based on analyses of microbial communities and microbial processes. However, they did not directly consider differential adaptations in particular microbes, i.e, trait-based analyses (Martiny *et al.*, 2015) in a way that parallels the core auto-ecological foundation of the Noy-Meir PRP for plants. The microbially based contributions thus remain a self-contained black box that offers none of the interpretive granularity that can be ascribed to plant communities. For example, the time scale for pulse responses is known to be much shorter for microbial than for plant processes (Collins *et al.*, 2014), but while we can explain differential plant response times and thresholds on the basis of plant rooting depth, no such granularity can yet be achieved for microbes.

A successful strategy of scientific progress has been the borrowing of pieces of theory and their mathematical models from sister disciplines. Early on, concepts borrowed from the cost-income theory from economics were applied to the evolution of resource allocation between leaves and roots in plants of arid environments (Orians & Solbrig, 1977). Noy-Meir developed his PRP simultaneously under the intellectual influence of the International Biological Program (Boffey 1976). The cost-income theory is thus implicitly embedded in the PRP. Organisms need to utilize resources in the form of stored nutrients and energy to support a shift from quiescent to active state, to prepare for an eventual safe return to dormancy, and to mitigate environmental insults during the inactive state. Plants deploy new roots and leaves to capture resources after a rainfall pulse; their seeds germinate based on carbon reserves accumulated pre-emptively during the times of plenty. The PRP predicts that the resources acquired during the pulse will be enough to replenish storage to be able to restart the cycle at the onset of the next pulse, and result in some non-zero net growth during the pulse. Variability of the duration of the pulses determines whether enough resources are acquired to fulfill the needs. Short pulses may end up in the

consumption of more resources than can be acquired, leading to organismal or population demise. Long pulses will certainly offset the initial investment and yield a positive effect on storage. Thresholds for shifts from quiescence to active state interacting with the length of pulses thus determine the outcomes for individuals and populations.

It is the intention of this contribution to probe if the core tenets in the PRP find applicability in microbial biology, a discipline that has become much more conspicuously important for the ecology of drylands than might have been surmised at the time, and one that now has experienced at least some advances to attempt such an exercise. Recent contributions show that it is indeed possible to attain general theoretical frameworks that are applicable to both micro- and macroorganisms when they are derived from basic, universal core tenets, as is the case with the principles of biological seed banks (Lennon *et al.*, 2021). Broadening the PRP beyond plants has been very important in guiding integrative research in drylands and developing new tools for holistic dryland management. Our central questions are: 1) Is the PRP applicable to microbes at large? 2) Is there a universal PRP that can be applied from microbes to plants? and 3) What are the organismal adaptations in plants and microbes that allow them to manage different sized pulses? Since the PRP was first developed with plants in mind, we highlight plant-microbe contrasts in the process. Here, we introduce a new conceptualization: the importance of reserve management style as the basis for organismal adaptations to cope with pulsed resource availability. We frame it with a mathematical model, evaluate its predictions in the light of knowledge of organismal biology, and explore the consequences and applicability of the generalized paradigm.

Modelling the PRP: nature and consequences of pulsed resources

We reframed the PRP to make it generically applicable but preserving its basic tenets. Succinctly, biological activity in drylands is strongly determined by pulses of water availability (Noy-Meir, 1973), and this challenge is met by organisms through the accumulation of reserves during the pulse that are then used to power transitions into and out of dormancy. The reframing is still based on the tenet that all organisms base their response to pulses on the accumulation of reserves, but we introduce the concept that organisms can differ in their reserve management

style along a continuum between two strategies. At one end of the continuum, what we call “Nimble Responders (NIRs)” are organisms that transition swiftly in and out of pulse utilization mode. To achieve this, however, they allocate a certain proportion of their metabolism and resources to maintain a constant, constitutive physiological readiness for inter-pulse conditions, and to ensure that metabolic systems are inherently hardy and protected at all times. Such level of constant readiness comes at the cost of building permanent, constitutive reserves, thus depressing their growth potential (and rate) from a theoretical maximum; they are inherently slow growers. At the opposite end, “Torpid Responders (TORs)”, while they do allocate portions of their resources as reserves to prepare for quiescence, they only do so as a pulse nears an end. These can be understood as late-pulse investments. Consequently, they can allocate recently acquired resources fully to growth processes during much of the pulse unconstrained by allocation to reserves, and they grow swiftly during it. Because of their low level of constitutive readiness, the lag times for transition to dormancy and back into growth among TORs are long, in that reserves need to be mostly synthesized from scratch towards the end of a pulse and then retrofitted into growth-promoting biomass at the beginning of the next pulse. To continue the financial metaphor, NIRs can be understood as conservative investors, focused on certainty of returns that are not high but are frequent, while TOR would be akin to risky investors whose strategy relies on high returns that occur rarely. It is important to realize that specific organisms will fall within the continuum between the extremes exemplified in the NIR and TOR acronyms. The distinction will be most properly used when comparing the relative position of an organism along this continuum, and probably most useful when comparing the relative character of pairs of organisms.

An explicit mathematical model based on the ideas in the previous paragraph is presented in Supplementary Materials, the main formulations of which are gathered in BOX 1. Its input parameters, outputs and predictions are discussed in the following paragraph.

The duration of the pulse is divided into three periods: transition from quiescence, growth phase and transition to quiescence. The level of “constant readiness” for quiescence is gauged by the parameter α , which constitutes the central parameter in the model, defined and calculated as the proportion between reserve biomass and growth-yielding biomass maintained during the growth

phase in the pulse. It remains constant within it, and growth must be positive, the level of constant readiness will vary between 0 minimally, and maximally approach 1. Organisms approaching the NIR end with high constant readiness will have high α , and TOR-like organisms will be characterized by low α . The level of investments in reserves needed to ensure successful transitions in and out of dormancy is gauged by the parameter, β , which is defined and calculated as the ratio of growth-yielding biomass to reserve biomass reached at the end of the pulse. Organisms that do not reach β by the end of a pulse will not be viable at the next iteration. Nothing prevents an organism to invest very heavily in β , and its maximal values are principally not constrained, but if these reserves are retrofitted into growth structures at the next pulse with reasonable efficiency (i.e., above 30%), β will typically take values below 3. The instantaneous growth rate (μ) that is possible at any one time during the growth phase in a pulse is dependent on α , being depressed from its maximal value by the resources allocated to constant readiness. The net yield of growth, defined as the ratio of growth enabling biomass at the end of a pulse to that at its beginning is, however, dependent on both α and β . The dynamics of growth-enabling biomass and reserve biomass during a pulse under this framework model are depicted in Fig. 1A. A comparative depiction of the dynamics of growth during a pulse for end-member organismal types is in Fig. 1B. Again, NIRs are characterized by low μ , but high α , while TORs by high μ but low α .

Relevant model outputs are the duration of the transition periods and growth phase, the net new growth yield after completion of a pulse cycle, and the minimal duration of a pulse required for viability. Their formulation as a function of input parameters is in BOX 1. The duration of the growth phase is determined by the duration of the pulse minus the duration of the necessary transitions. Pulse duration must exceed the duration of transitions for organisms (or populations) to attain net growth. While the point has been made that transitions are energetically costly for both plants (Gremer & Sala, 2013) and microbes (Schimel, 2018), they are also costly in terms of time, particularly when active time is at a premium. Hence, we also define a *minimal pulse duration* that allows for completion of the necessary transitions. Should a pulse last less than this minimal duration, viability will be compromised and the resuscitation strategy will fail.

The model predicts that: 1) Transition times decrease with increasing constant readiness reserves (α) and increase with increasing end-of-pulse reserves (β); only in the case in which α tends to β , they tend to 0, which biologically corresponds to the case in which virtually all reserves needed for transition are always present. 2) The minimal duration of the pulse needed for viability decreases with increasing constitutive readiness (Fig. 2). 3) Increasing the amount of end-of-pulse reserves (β) lengthens minimal pulse duration for viability.

In terms of growth yields as a function of pulse duration (Fig. 3), the model predicts that: 1) The more an organism tends to the NIR end-member, the more it will benefit from a regime of short pulses whereas tending to the TOR end, will benefit from longer pulses. 2) Investments in end-of-pulse reserves (β) result in advantages in growth yield regardless of pulse duration, as long as the minimal pulse duration is exceeded. 3) The return of late-pulse investment becomes increasingly negligible for very long pulses. In general terms, the constant readiness of NIRs is only beneficial when pulses are short, while late-pulse investments matter more when pulses are intermediate in duration. When pulses are so long as to lose their “pulsed” character neither type of adaptation is beneficial, consistent with the PRP tenet that the gathering of reserves is a characteristic selected for only under pulsed regimes of growth.

While we have expressed pulse duration, rather unintuitively, as the inverse of $\mu_{\max}$, these units have a biological meaning. In exponential growth $1/\mu_{\max}$ represents the time it takes for a population to grow by a factor of e . It is related to the (minimal) doubling time, D , as $D = \ln 2/\mu_{\max}$. So, in biological terms, NIR organisms will have an advantage in pulses that are shorter than some $6 D$ (below some 10 times $1/\mu_{\max}$; Fig. 2). For bacteria, while there is considerable variability, average doubling times are around 5 h (Weissman *et al.*, 2021). Thus, for bacteria, recurrent pulse durations shorter than a day will benefit only NIRs, and above that, TORs will do better, but “pulses” exceeding a week, will not benefit either type. For plants, the analogous whole-plant relative growth rates (RGR) vary between 0.1 and 0.4 d^{-1} (Price & Munns, 2020), and we can take 3 days as a typical doubling time. NIR plants will benefit from (soil) water pulses shorter than 18 days, but that will be insufficient for TOR plants. Pulses of water availability that exceed many months will not yield differential benefits to either type.

Importantly, however, all these predictions are derived from very simple, generic tenets that do not involve specific plant functional traits, so that they are therefore universally applicable. Pulse duration/size bestows benefits differentially between NIRs and TORs, and its variability can principally drive organismal specialization, in turn supporting differentiated ecosystem-level outcomes, which is a fundamental characteristic of the PRP (Schwinning *et al.*, 2004). The predictions thus logically imply that shifts in pulse size distribution range will impact the functional types of organisms that can effectively grow, the spatial extent of their populations and their dynamic fate under climates changing in time or space. Experimental evidence consistent with this prediction has been presented: imposed treatments with decreased average rain pulse size result in swift and very marked shifts in community composition of primary producers of biological soil crusts, favoring cyanobacteria over mosses (Reed *et al.*, 2012), and favoring some species of cyanobacteria over others (Fernandes *et al.* submitted). Similarly, the predicted shift in plant species composition under regimes of differing pulse size have been presented (Jones *et al.*, 2016). Traits that might implicate differential management of reserves among losers and winners, however, were not directly quantified in any of those cases.

On the other hand, it is not difficult to find principally NIR-like and TOR-like cases among arid-land plants. For example, perennial grasses such as *Bouteloua gracilis* that dominate enormous areas of North America have shown a remarkably fast response to precipitation pulses. Not only leaf water status and photosynthesis but also root growth (Lauenroth *et al.*, 1987) rapidly shift in a few hours after a rain event into an active state, returning to quiescence a few days after. These grasses invest constitutively in non-structural carbohydrate reserves (Menke & Trlica, 1983), lignocellulose, and in hardy crown tissue structures containing buds and tillers that together allow fast onset of growth. Yet, they produce only moderate amounts of seeds. Annual grasses that dominate California grasslands, by contrast, are examples of TOR-like plants: comparatively, they grow swiftly without conspicuous investments in structures dedicated to improving survival under inter-period conditions, but they do so only during rather large pulses of precipitation (Huenneke & Mooney, 2012). Towards the end of the pulse their physiology quickly turns into the all-out production of reserves in the form of large amounts of seeds. The ultimate question for us remains: is there evidence that microorganisms also fit in this framework? Since its premises are only a pulsed nature of growth, the reliance on reserves as

strategies, and the differential management of reserves by specific types, the question translates essentially to finding evidence that microbes rely centrally on reserve-building and to find a functional differentiation between NIRs and TORs among them.

Microbial traits in drylands

Before we embark on the attempt to characterize traits of dryland microbes, we should consider that climatic definitions were not made with them in mind. Some microbes greatly exceed the perceived limits of temperature and water availability that underlay climatic cutoffs (Rothschild & Mancinelli, 2001, Schulze-Makuch *et al.*, 2018), and spatial environmental variation within a single climatic region can create non-compliant microniches. Texturally coarse soils of mesic climates, for example, unable to retain meteoric water inputs for very long do often sustain microbial communities typical of deserts in temperate climates (Smith *et al.*, 2004). In hyper-arid settings, the presence of surface pebbles that locally retard soil water evaporation allow the formation of hypolithic microbial communities, embedded in an otherwise barren landscape (Schlesinger *et al.*, 2003, Warren-Rhodes *et al.*, 2006). Thus, paradigms that may ensue from the study of microbial adaptations to aridity will find full applicability outside of climatically understood drylands and will fail to apply in some instances within them. One should apply the concept of aridity in agreement with the implied outcome of biological activity hindrance by water scarcity. Still, several representative characteristics of dryland plant communities do in fact find parallels in their microbial co-inhabitants. A direct evaluation of differential genomic capabilities as well as comparative surveys of microbial distributions reveal that microbial communities and their member microbes are uniquely adapted to arid conditions, as are desert plants and animals. Global distributional surveys of soil bacteria clearly point to a compositional differentiation in drylands from those in other climates (Angel *et al.*, 2013, Neilson *et al.*, 2017, Delgado-Baquerizo *et al.*, 2018, Schulze-Makuch *et al.*, 2018), a pattern that seems to involve preferentially rare species, i.e. species with a narrow-niche (Bickel & Or, 2021). These are traits they share with plant and animal communities. In fact, for a few specific microorganisms, we have sufficient evidence that their distribution is constrained to arid environments, implying a maladaptation to other climates (Hector & Laniado-Laborin, 2005). And yet, as it is true for microbes in most environments, we know relatively little about the specific nature of these differential adaptations, given that most microbial ecology efforts are not geared to establishing

the “natural history” of particular microbes, their auto-ecology, but rather to establish emergent properties of microbial communities taken as black boxes. But it is precisely these organismal auto ecological traits that comprise the central pillars of the PRP. At most, changes in community composition can be used to infer trait-based patterns assuming that some traits have a phylogenetic correlation. But this exercise is fraught with perils, in that phylogeny seems to underpin certain traits more strongly than others and also differentially so among major microbial groups (Martiny *et al.*, 2015). The opposite concept is that of convergent evolution in which similar traits evolved along different evolutionary paths both in plants (Orians & Solbrig, 1977) and microbes (Garcia-Pichel & Wojciechowski, 2009)

Microbes in arid conditions do lead a life characterized by rare pulses of activity embedded in a regime of suspended animation (Lennon & Jones, 2011, Schimel, 2018). Because of the short generation times of microbes, community composition can change dramatically even within the duration of a single pulse, based on the resuscitation of dormant, rare species (Aanderud *et al.*, 2015). This implies that selective forces acting on traits that sustain transitions from dormant to active states are at play. Metagenomic (Le *et al.*, 2016) and metatranscriptomic (Rajeev *et al.*, 2013) analyses of arid soil bacterial populations speak of the crucial importance of the capacity to repair genetic damage accumulated during inactive periods for an effective recovery from dormancy. Activation of DNA repair seems to be the absolute priority inasmuch as they constitute the very first wave of gene expression upon microbial rehydration (Setlow, 2007). The studies carried out on two desiccation-resistant model bacteria, *Deinococcus* (Cox *et al.*, 2010) and *Chroococcidiopsis* (Billi *et al.*, 2000) tell us a similar story about the relevance of damage repair. Adaptations to avoid photodamage, such as the synthesis of passive sunscreen compounds (Garcia-Pichel *et al.*, 1992), or the increase in cellular ploidy to attain genomic redundancy (Cox *et al.*, 2010, Sukenik *et al.*, 2012), also speak of the importance of adaptations to increase overall fitness by decreasing mortality during quiescence. While synthesis of these components is accomplished during active periods of growth, their contribution to fitness takes place under metabolic dormancy, when active repair does not take place. The sunscreen scytonemin, for example, is common in cyanobacteria that thrive under pulsed growth conditions, including those from soil crusts and epilithic environments (Garcia-Pichel & Castenholz, 1991), but has been recurrently lost through the evolution of the Phylum Cyanobacteria in clades that adapted to

more constant environments (Garcia-Pichel *et al.*, 2019). The decoupling of light-harvesting systems from reaction centers in desert microbial phototrophs constitutes another example of a preventative strategy (Bar-Eyal *et al.*, 2015), and so does the migration towards environmental refugia in anticipation of desiccation (Pringault & Garcia-Pichel, 2004). Similarly, significant investment into spore formation (Setlow, 2007) is common in saprophytic fungi and in at least two phyla of bacteria, the Firmicutes and the Actinobacteria (Lennon *et al.*, 2021). These examples clearly speak for an anticipatory, integrative coordination between the “system states” of quiescence and active growth, a shift that can occur rather rapidly at the physiological and genetic levels (Rajeev *et al.*, 2013, Oren *et al.*, 2019). Thus, microbes adapt to the pulsed nature of their environment, rather than to either the active or inactive phases in it. This brief review of microbial life strategies suggests that a preemptive accumulation of reserves (in the form of cellular machinery and energy reserves to fuel repair upon activation, or as investment in costly secondary metabolites to avoid damage) could well play a role in the swift and effective use of short pulses of hydration and activity; and may in fact underpin the adaptation of microbes to life in arid lands.

Size differentially affects how microbes and plants cope with a pulsed environment.

The small size of microbes imposes constraints and opportunities that differ significantly from those affecting plants. Relevant processes scale with size (L), oftentimes because of the differential scaling of body volume (L^3) to surface (L^2). In any attempts to test how the PRP applies to microbes, one should take those effects into account. For example, because the usefulness of sunscreens depends directly on the thickness of the teguments they are laid onto, plants can use sunscreens much more efficiently for photoprotection than microbes can (Gao & Garcia-Pichel, 2011). Because conductive heat transfer scales inversely with size (Planinšič & Vollmer, 2008), very small organisms equilibrate temperature with its surrounding virtually instantaneously. Temperature homeostasis simply cannot be a microbe’s forte: microbes must evolve to endure temperature shifts unscathed instead. Mass transport is very strongly scale sensitive. At small scales, a microbe’s environment becomes essentially stagnant, diffusion becoming the main mass transport vehicle; but diffusion’s effectiveness scales with L^{-2} . This is why bacteria do not need internal transport structures, and why metabolite exchange among

microbes at short range is quite effective, requiring little metabolic effort. Desiccation can be understood in similar physical terms, as the diffusional loss of water in a gradient of water potential, and hence fractional water loss scales with L^{-2} (Jakubczyk *et al.*, 2012, Carrier *et al.*, 2016). Again here, microbial cells will tend to equilibrate with their immediate surroundings virtually instantaneously and microbial cells will be as wet as their environment is. Attempting to keep water inside a microorganism by retarding evaporation using non-diffusive teguments (as some plants do using cuticular waxes) is principally a lost cause.

An important caveat for the generalizations above, however, is that aggregation of microbial cells into larger, coherent structures such as colonies or biofilms can reverse these physically imposed opportunities and limitations. Nutrient supply can be limited by diffusion when microbes come together into mm-sized aggregates or biofilms (Garcia-Pichel *et al.*, 1999). When they do, they typically create microenvironments around such aggregates (Garcia-Pichel & Belnap, 2001) because diffusion is insufficient to release their metabolic byproducts. In some extreme cases, such macroscopic aggregates can cause turbulent transport of nutrients through motility (Fenchel & Glud, 1998), increase the albedo and equilibrium temperature of soil surfaces (Couradeau *et al.*, 2016), or retain moisture for some time after a rain event (Scherer & Zhong, 1991). Macroscopic aggregates of microbes must be independently evaluated for the relevance of such effects.

Do microbes also use activity pulses to gather reserves in preparation for quiescence?

Microbes do produce organic and inorganic storage reserves, typically in the form of polymers that help them avoid high cellular turgor pressure: polyglucose (glycogen, starch) and poly- β -hydroxyalkanoates (PHAs) are carbon reserves. These type of reserves are prevalent among microbes (Mason-Jones *et al.*, 2021). More specialized polymers, like cyanophycin, store carbon and nitrogen, and polyphosphates store inorganic phosphorous (Kolodny *et al.*, 2006). Colorless sulfur bacteria can even accumulate electron donors like polymeric sulfur and acceptors like nitrate (Schulz *et al.*, 1999). Polymerization and mobilization of all of these reserves is responsive to pulses in availability of the respective nutrient (Dawes & Senior, 1973), in patterns suggestive of a prioritization of storage over growth when resource depletion is imminent (Mason-Jones *et al.*, 2021). The gathering of reserve polymers is generally considered a major physiological trait enabling microbial dormancy and the

formation of seed banks (Lennon & Jones, 2011). A genetic ability to produce abundant reserves, correlates in specific microbes with resistance to stress conditions (Madueño *et al.*, 2018) and can demonstrably support resuscitation from dormancy (Klotz *et al.*, 2016). Recent studies of gene expression in field populations of the cyanobacterium *Microcoleus vaginatus* from soil crusts during wetting/desiccation pulses showed the importance of reserve compounds in the context of overall gene regulatory acclimation: genes for cyanophycin and polyphosphate synthesis were expressed heavily during the “growth”, wet phase (see Fig.1), whereas those for the mobilization of both glycogen and polyphosphate reserves were strongly upregulated with the onset of desiccation, in the “transition to quiescence phase” of Fig.1. Direct measurements and metabolic simulation have shown that *M. vaginatus* allocates more fixed carbon to polymers constitutively than other cyanobacteria (Jose *et al.*, 2018), indicating that this microbe tends to be a NIR type, which is consistent with field experimentation (Fernandes et al, submitted) . Both these facts are consistent with the pulse-reserve hypothesis as it pertains to carbon and nutrients, the reserves accumulated during wet times allowing the preparation for successful dormancy (i.e., anticipatory regulation) during drought. Other microbes are known for the accumulation of specific resources in preparation for desiccation or exit from quiescence phases (Klotz & Forchhammer, 2017). The soil actinobacterium *Rhodococcus* upregulates the formation of ectoin (a compatible solute), and proteins to detoxify oxygen stress (LeBlanc *et al.*, 2008). Such investments can be significant. UV sunscreen compounds, like cyanobacterial scytonemin, can make up investments in the order of several percentage points of a cell’s dry mass, becoming useful in comparison to active repair mechanisms only during quiescence (Gao & Garcia-Pichel, 2011) and its biosynthesis is enhanced by desiccation (Fleming & Castenholz, 2007). Glycogen or PHA can be accumulated to more than half of a cell’s dry weight (Klotz & Forchhammer, 2017, Madueño *et al.*, 2018). Such level of accumulation would speak for associated values of the parameter β in our model easily exceeding unity.

The developmentally sophisticated formation of desiccation-induced spores (Sukeník *et al.*, 2015) (Setlow, 2007), a strategy shared by fungi and several bacterial phyla, represents perhaps an extreme case of all-out late-pulse allocation to reserves (typical of TORs with low α) that enables extremely long quiescence periods. The trade-off here is that a relatively long new pulse with copious resources is needed to allow for an equally complex process of germination (Stewart *et al.*, 1981, Dworkin & Shah, 2010) before new resources can be effectively tapped, as predicted by our model. Thus, as in plants, not only do microbes prepare for dormancy through the gathering of resources, but examples

of microorganisms adapted to either short or long pulses that manage these reserves differently can also be found.

Soil segregates between microbial NIRs and TORs

In Noy-Meier's framework, soil acts as a water repository that significantly extends water availability beyond the precipitation pulse, for organisms that can tap it, (Fig. 4) and is a central consideration in the original and subsequent refinements of the paradigm (Ogle & Reynolds, 2004). As one proceeds down the soil profile, water content suffers from diminished inputs (infiltration inputs will require larger pulses) but benefits from more moderate evaporative losses, so less water reaches deep layers but there it lingers over longer periods. So, pulse duration increases with soil depth (Sala *et al.*, 1992). This differential distribution of water in the soil profile translates into a force for plant diversification, where NIR-tending functional types specialize in tapping surficial resources whereas TOR-like shrubs utilize mostly deeper water (Jackson, 1999). But, how does this translate to soil microbial populations? We have seen how in principle the duration of a pulse for a microbe will tend to be as long as the water is available in its immediate surroundings. Undoubtedly, system responses that rely on microbially mediated processes are much faster than those mediated by plants (Austin *et al.*, 2004). Consistent with long known empirical evidence (Linn & Doran, 1984), soil microbial activity should follow the dynamics of soil water content along the profile and in time (Fig. 4). We can thus expect that microbes will function for short periods at the surface (NIR territory), and for longer periods as they move down the profile (increasingly TOR turf). In fact, it is those spore formers in the Firmicutes and the Actinobacteria (TOR-like organisms) that tend to dominate zones deep in the soil profile (Fierer *et al.*, 2003), where high water content episodes are rare but once they happen, they last for long time. In soil surface communities such as biocrusts, by contrast, TOR spore-formers are typically exceedingly rare under normal conditions (Garcia-Pichel *et al.*, 2003), although veritable blooms of spore-formers can be brought about by long flooding of these crusts (Karaoz *et al.*, 2018). Typical soil-surface communities, like biocrusts, are inhabited by communities that respond swiftly, within minutes, to pulses (Scherer & Zhong, 1991, Garcia-Pichel & Belnap, 2001). The point has been made that the ecosystem contributions to carbon cycling of such communities is particularly important under regimes of short pulses (Cable & Huxman, 2004). Further, even within surface communities, plant-interspaces are prone to

experience more intensely pulsed conditions than the soil under plant canopies. Trait-based comparisons of microbial communities in these two contrasting environments from an arid setting show a significant enrichment of spore-forming microbes in soil under plants (more TOR-like in our framework), even when generic traits to resistance to desiccation were more enriched in the interspace soils (Goberna *et al.*, 2014).

The mechanisms by which this is accomplished differ between plants and microbes. The shorter generation times of microbes allow this to take place at the level of community assembly, rather than just as evolutionary eco-physiological diversification. In fact, experiments show that even short-term variations in aridity can exert rather swift microbial community shifts in a variety of settings (Rothrock Jr & Garcia-Pichel, 2005, Castro *et al.*, 2010, Barnard *et al.*, 2013, Liu *et al.*, 2019). In a mesoscale experimental set up, soil crust cyanobacterial communities suffered stark shifts in organismal dominance within a few years of either a decrease in overall precipitation or a 2 month delay in the onset of the rainy season (Fernandes *et al.*, 2018), promoting dominance of NIR-like, drought-resistant *M. vaginatus* over other cyanobacteria. These dynamic compositional shifts find consistent parallels in the geographical distribution of the same cyanobacterial taxa along varying climates (Fernandes *et al.*, 2021). The patterns reviewed above indicate that while the effects on diversification operate through alpha-diversity in plant communities, they do so through beta-diversity along the soil profile in microbial communities. In sum, both in plants and in microorganism, the pulsed nature of water distribution in the soil is a force for niche partitioning and evolutionary diversification, as postulated by Noy-Meir.

Formally testing the model

We have sought here to assess the NIR/TOR model for consistency with current organismal knowledge. While the phenomenology reviewed is consistent with its predictions, it is only indirectly and qualitatively so, and it encompasses only the few organismal types whose biology was informative enough. It will be important in the future to test the model more formally, quantitatively, and generally. A conceptually simple experimental test could make use of imposed variations in pulse duration and pulse number as the cumulative pulse time is kept constant, as has been previously used to assess effect at the community or ecosystem level (Jones

et al., 2016)(Fernandes *et al.*, submitted), but with a focus on quantitative determination of the main parameters in the model: μ , α and β . The expectation here is that experimental increase in pulse frequency and reduction in pulse duration will result in changes in microbial community composition that favor the presence of organisms with elevated α and lower μ . Alternatively, one could seek a correlative validation by comparing the average NIR vs. TOR character in locales selected along geographical gradients of pulse-size distribution. Naturally the duration of experimental treatments will have to allow for differences in generation times between plant and microbes. In the case of microbes, determination of α , β and μ can be best performed using relevant isolates in culture. For plants, single-species specimens for analyses can be easily obtained from the field (Gremer & Sala, 2013). Quantification of α and β is rather straightforward using biochemical analyses for known reserve compounds (Del Don *et al.*, 1994, Martínez-Vilalta *et al.*, 2016) during the appropriate time (growth phase for α , or initial quiescence phase for β).

Organismal traits can also be principally derived from (meta)genomic information directly from natural microbial communities. For example, genomically-coded information can be used to indirectly gauge habitat breadth (Barberán *et al.*, 2014), maximal growth rates (Weissman *et al.*, 2021), or nutritional modes (Chen *et al.*, 2021) of specific phylotypes. Further, comparative analyses of genomic complexity in the genes underlying particular traits provides proxies for the relative importance of a given trait in a given setting (Cao *et al.*, 2020). In some cases, organismal traits can be assigned to particular phylotypes on the basis of sequence similarity to known organisms (Goberna *et al.*, 2014, Couradeau *et al.*, 2019), making it principally possible to derive organismal traits from the most common form of community data analyses (i.e., 16S rRNA amplicon sequencing), although this requires assumptions of phylogenetic conservation that are far from guaranteed (Martiny *et al.*, 2015). Metagenomic approaches are much preferred in this context. To test predictions regarding the NIR-TOR continuum, genomic/transcriptomic proxies for its three main parameters (μ , α and β) can be readily envisioned. Ribosomal codon use bias can be used to gauge the maximal growth rates commonly realized by an organism in its habitat, as it reflects adaptations of the protein synthesis machinery to those maximal rates. This will gauge our parameter μ (rather than our $\mu_{\max}$, which defines a theoretical maximal growth rate

for any organism under a given set of conditions and resources). While the relative importance of reserves in a given microbe can potentially be ascertained by the presence, relative abundance and complexity of the genes that code for their synthesis and mobilization (Rajeev *et al.*, 2013), the direct derivation of proxies for α and β , is probably more complex, if not impossible, since the genetic underpinning of constitutive (α) and end-of-cycle (β) reserves is likely shared. An assessment of relative gene expression levels during growth and transition phases will be required, which will necessitate the use of time-resolved (meta)transcriptomics during actual pulse experiments.

Conclusions and Outlook

Yes, the PRP works from microbes to plants. However, the mechanisms that evolved to cope with an environment characterized by resource pulses followed by prolonged periods of quiescence are different for microbes and plants. Size determines the mechanisms that make organisms thrive in this highly variable and extreme conditions. We do find examples approaching NIR and TOR organisms in both plants and microbes. In many regards, Noy-Meir's vision of the pulse-reserve dynamics shaping the natural history of desert organisms is applicable to microbes, which show a diversity of adaptations much richer than he could have envisioned when he lumped microorganisms under the term "poikilohydric". These adaptations are in many regards convergent with those of plants, although they are often modulated by scaling constraints. The PRP clearly holds across levels of biological organization for carbon reserves and for specialized structures when understood as a function of strategies to manage necessary reserves (Fig 5). The consequences of a pulsed water regime for functional diversification hold across organismal boundaries but operate largely through organismal diversity in plants and more intensely through community assembly in microbiomes.

While the current formulation of our model suffices to predict many of the predicted outcomes of the PRP, it does not explicitly include two aspects of arid land organismal adaptations that may *a priori* be considered relevant: the capacity for acquisition of water reserves and the length of periods in between pulses. Acquisition of water reserves serves the purpose of effectively lengthening the pulse duration and is a common adaptation among dryland plants like cacti and

euphorbias. The issue with water reserves is much tougher for microbes than for plants, because of the size constraints discussed above, although extracellular polysaccharide investments may slow rates of water loss (Roberson & Firestone, 1992, Chenu, 1993, Hart *et al.*, 1999). This is clearly so in microbes that build macroscopic thalli like *Nostoc commune* (Scherer & Zhong, 1991), or in microbial assemblages that attain sufficient mass, but are unlikely to make much of a difference for single, typical microbial cells. This may very well be behind the well-known fact (Potts, 2001, Alpert, 2005) that only small organisms (or small independent parts of plants, like seeds) can truly be anhydrobiotic, that is survive a temporary loss of all (or most) of their water, since reliance on anhydrobiosis is the only viable solution for small beings. Drought resistance in macro-organisms, by contrast, is always dependent on preventing water loss. Increasing length of pulse inter-periods will decrease the capacity of dormant cells to resuscitate as they accumulate environmental insults that will have to be repaired. In our framework, this will mean that organisms faced with long droughts will experience a decrease in the efficiency with which reserves can be retrofitted into growing biomass, which we had assumed to remain constant and high. This is likely to be countered by increases in β to make up for the loss in efficiency, which in turn will increase the minimal pulse size for viability, and thus likely affect NIR types more negatively than TOR types. These aspects should be given more detailed attention in future work.

Given that continental microbial ecosystems similar to those now present in drylands are known to have existed (Simpson *et al.*, 2013, Beraldi-Campesi *et al.*, 2014) and to have driven global biogeochemical cycles (Thomazo *et al.*, 2018) since the mid-Precambrian, long before the advent of land plants, perhaps the fact that microbes follow the PRP should not come as a big surprise, since opportunity makes the thief. An apparently universal differential aspect of the biology of living organisms under arid regimes is that fitness under pulsed conditions in a background of water scarcity becomes a strong function of strategies to prevent death during periods of quiescence, whereas mechanisms geared towards promoting fast growth become less relevant than they might be in mesic environments. In other words, desert organisms, including microbes, can be expected to be hard to grow but hard to kill. Microbes probably found that out first, the hard way.

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FIGURES AND LEGENDS

Fig. 1. A: Modelled dynamics of growth-yielding biomass (G) and reserves (R) during a pulse of resources with explicit transitions between quiescence and growth and back to quiescence. Important parameters are intrinsic maximal growth rate ($\mu_{\max}$), the ratio of biomass allocated constantly to reserves over that allocated to growth during growth (constant readiness, α), and the ratio of biomass allocated to support transitions over that allocated to growth at the end of the pulse. Times for transition are dependent on the previous parameters. B: Differential strategies of management of reserve investment result in distinct functional adaptations: NIRs and TORs. NIR organisms invest conservatively in preparation for quiescence (high α), and can respond swiftly (short transition times), at the expense of lower growth rate (μ), whereas TORs invest with higher risk (low α), need longer transition times but can grow fast during favorable times. Explicit mathematical model equations are in Supplementary Materials.

BOX 1. Formulations for growth dynamics and main output parameters

Dynamics of biomass during growth phase

Growth-yielding biomass $G(t) = G_1 e^{(1-\alpha)\mu_{max}(t-t_1)}$

Reserve biomass $R(t) = \alpha G_1 e^{(1-\alpha)\mu_{max}(t-t_1)}$

Growth yield after a complete pulse

$$\frac{G_3}{G_0} = \left(1 + \beta - \frac{\alpha(1 + \beta)}{1 + \alpha}\right) \left(\frac{(1 + \alpha)e^{\mu_{max} t_3}}{1 + \beta}\right)^{(1-\alpha)}$$

Phase and pulse duration

Transition to growth $t_1 = \frac{1}{\mu_{max}} \ln \left(\frac{\beta(1 + \alpha)}{\alpha(1 + \beta)} \right)$

Transition to quiescence $(t_3 - t_2) = \frac{1}{\mu_{max}} \ln \left(\frac{\beta}{\alpha} \right)$

Growth phase $t_2 - t_1 = t_3 - \frac{1}{\mu_{max}} \ln \frac{1 + \beta}{1 + \alpha}$

Minimal pulse for viability $t_{3,min} > \frac{1}{\mu_{max}} \ln \left(\frac{\beta}{\alpha} \right)^2 \left(\frac{1 + \alpha}{1 + \beta} \right)$

Fig.2. Minimal pulse duration for viability ($t_{3,min}$, expressed as multiples of the inverse of μ_{max}) as a function of level of constant reserve investment (constant readiness, α) for various values of late-pulse reserve investment (β).

Fig. 3. Dependence of growth yield (defined as fold increase in G over the duration of a pulse) on pulse duration (expressed as multiples of the inverse of $\mu_{\max}$), for various values of constant readiness α (left) and late-pulse investments β (right). Vertical bars indicate minimal pulse duration as per Fig. 2. Only moderate yields are ever attained with high α , but positive growth is attained even with very short pulses. Higher yields can be attained by increasing β , but at the expense of higher thresholds for viability, and the beneficial effects become irrelevant for very long pulses.

Fig. 4. Noy-Meier's concept of the plant-system responses (shaded areas) to pulsed water resources (black bars) in the left panel, with its translation to microbial responses for NIR-like microorganisms close to the soil surface (middle panel) and for TOR-like microorganisms deeper in the soil profile (right panel). Panels a to c represent different pulse regimes.

Fig. 5. Conceptual abstraction of the organismal strategy continuum for the management of reserves that result in optimal returns under pulsed activity regimes of varying pulse length. Most organisms will find themselves in the continuum between nimble responders (NIR) and torpid responders (TOR).

SUPPLEMENTARY MATERIAL

Expanding the Pulse-reserve paradigm to microorganisms on the basis of differential reserve management strategies

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Explicit modeling of pulsed growth

1. Growth phase

Let's assume that during growth episodes a proportion of the total resources are converted into biomass capable of growth while the rest is allocated to reserves. Let us name the growing biomass G and the reserve biomass R . Let us also assume that growth is exponential. If no reserves are allocated at all, then growth is maximal, $\mu_{\max}$, as determined by both inherent physiological constraints, and the growth dynamics will follow the differential equation:

$$\frac{dG}{dt} = \mu_{\max} G \quad (\text{Eq. 1}).$$

But if the proportion of biomass allocated to reserves is α , then G will instead follow

$$\frac{dG}{dt} = \mu_{\max} (G - \alpha G) = \mu_{\max} (1 - \alpha) G \quad (\text{Eq. 2}).$$

Thus, G will growth with a smaller, but also exponential, rate and

$$\mu(\alpha) = \mu_{\max} (1 - \alpha) \quad (\text{Eq. 3})$$

Note that because $\mu(\alpha) > 0$, $\alpha < 1$

In integrated form Eq. 2 becomes:

$$G(t) = G_1 e^{(1-\alpha)\mu_{\max} (t-t_1)} \quad (\text{Eq.4})$$

Where t is time, t_1 is the start time of the growth phase, and G_1 is the value of G at t_1 .

Since during the growth phase a constant proportion of G is allocated constitutively to resources, $R = \alpha G$, in this phase

$$R(t) = \alpha G_1 e^{(1-\alpha)\mu_{max}(t-t_1)} \quad (\text{Eq. 5})$$

Hence the reserves also grow exponentially keeping pace with the growing biomass.

2. Transition from quiescence into growth

Transitioning successfully from quiescent status to growth status requires resources that are proportional to the existing biomass G_0 at the beginning of the transition. Let β be this proportion, so that $R_0 = \beta G_0$. R is used to power this transition, including activities of damage repair, repurposing of resistance structures into growth-enabling structures and so on¹. We can assume that the rate of use of R is maximal and equivalent to the inherent maximal growth rate μ_{max} , $R(t)$ in this phase thus decaying exponentially. The decay in R during this transition will be given by:

$$R(t) = R_0 e^{-\mu_{max} t} \quad (\text{Eq. 6})$$

And it will proceed until R reaches the proportion of reserves typical of the growth phase, α . We note that by necessity $\alpha < \beta$, $0 < \alpha < 1$, and $\beta > 0$.

When this is reached, at t_1 , the organism is ready to switch into growth mode, starting with a G_1 that has increased from G_0 by the new growth-enabling biomass additions from mobilized reserves. Thus:

$$G_1 = G_0 + \beta G_0(1 - e^{-\mu_{max} t_1}) = G_0(1 + \beta - \beta e^{-\mu_{max} t_1}) \quad (\text{Eq. 7})$$

The end of the transition phase and the beginning of the growth phase occurs when $R(t) = \alpha G_1$. Substituting Eqs. 6 and 7 and solving for t , we find that

$$t_1 = \frac{1}{\mu_{max}} \ln \left(\frac{\beta(1+\alpha)}{\alpha(1+\beta)} \right) \quad (\text{Eq. 8})$$

Thus, the duration of the transition depends inversely on the maximal growth rate, and on the proportions of biomass allocated to reserves constitutively, α , and at the beginning of the pulse, β . The transition time decreases with increasing α and with decreasing β . As β tends to α , t_1 tends to 0.

¹ We will assume that all reserves are being used to build growth-yielding structures, and that this happens with an efficiency of 100%

3. Transition from growth into quiescence.

Upon sensing that the pulse is coming to an end, organisms must switch from growth mode into full reserve-gathering mode, so that by the end of the pulse, the proportion of reserves has increased from the constitutive α to the amount needed to support an eventual transition back to growth during a future pulse, β . This is accomplished by redirecting resources fully from growth to reserves, and growth stalls. After this time of reckoning, t_2 , G will remain constant at G_2 , and reserves will grow at full capacity following

$$R(t) = \alpha G_2 e^{\mu_{max} (t-t_2)} \quad (\text{Eq. 9})$$

until they reach the necessary level, $\beta G_3 (= \beta G_2)$

The anticipatory interval, $t_3 - t_2$, needed to attain this must satisfy

$$\beta G_2 = \alpha G_2 e^{\mu_{max} (t_3 - t_2)}$$

so that

$$(t_3 - t_2) = \frac{1}{\mu_{max}} \ln \left(\frac{\beta}{\alpha} \right) \quad (\text{Eq 10})$$

Thus, the duration of this anticipatory period, increases logarithmically with decreasing α and with increasing β . As α tends to β , it approaches 0.

4. Integrated dynamics through the pulse

The total growth during a pulse of duration t_3 comes from initial transfers from reserves and from actual new additions during the growth phase. The former is given in Eq. 7 and the latter can be calculated from the duration of this growth phase, $[t_2 - t_1]$. Eq. 8 gives us t_1 , and Eq 10 gives us $t_3 - t_2$, so that

$$t_2 - t_1 = t_3 - \frac{1}{\mu_{max}} \ln \left(\frac{\beta}{\alpha} \right) - \frac{1}{\mu_{max}} \ln \left(\frac{\beta(1+\alpha)}{\alpha(1+\beta)} \right) = t_3 - \frac{1}{\mu_{max}} \ln \frac{1+\beta}{1+\alpha} \quad (\text{Eq 11})$$

As α tends to β , $[t_2 - t_1]$ approaches t_3 . As α decreases, $[t_2 - t_1]$ decreases logarithmically with it.

It is then possible to express explicitly the growth during a pulse as a function of its duration, t_3 , given α , β , and μ_{max} ,

$$G_3 = G_2 = G_1 e^{(1-\alpha)\mu_{max} [t_2-t_1]}$$

where G_1 is given by Eq. 7, so that

$$G_3 = G_0(1 + \beta - \beta e^{-\mu_{max} t_1})e^{(1-\alpha)\mu_{max} [t_2-t_1]}$$

And where t_1 and $[t_2-t_1]$ are given in Eqs. 8 and 11, respectively, so that

$$G_3 = G_0(1 + \beta - \beta e^{-\mu_{max} \frac{1}{\mu_{max}} \ln \frac{\beta+\alpha\beta}{\alpha+\alpha\beta}})e^{(1-\alpha)\mu_{max} [t_3 - \frac{1}{\mu_{max}} \ln \frac{1+\beta}{1+\alpha}]}$$

Making $A = \frac{\beta+\alpha\beta}{\alpha+\alpha\beta}$ and $B = \frac{1+\beta}{1+\alpha}$, we get:

$$G_3 = G_0(1 + \beta - \frac{\beta}{A})e^{(1-\alpha)\mu_{max} [t_3 - \frac{1}{\mu_{max}} \ln B]}$$

$$= G_0(1 + \beta - \frac{\beta}{A})e^{(1-\alpha)\mu_{max} t_3 - (1-\alpha) \ln B}$$

$$= G_0 \left(1 + \beta - \frac{\beta}{A}\right) \frac{e^{(1-\alpha)\mu_{max} t_3}}{e^{(1-\alpha) \ln B}}$$

$$= G_0 \left(1 + \beta - \frac{\beta}{A}\right) \left(\frac{e^{\mu_{max} t_3}}{B}\right)^{(1-\alpha)}$$

$$\frac{G_3}{G_0} = \left(1 + \beta - \frac{\alpha(1+\beta)}{1+\alpha}\right) \left(\frac{(1+\alpha)e^{\mu_{max} t_3}}{1+\beta}\right)^{(1-\alpha)} \quad \text{Eq. 12}$$

5. Evaluation of minimal transition times

However, t_3 must minimally allow for both transition periods to take place fully, or otherwise the proportion of reserves will have decreased below the level needed to allow a successful resuscitation at the next pulse. Thus, this minimum duration, $t_{3,min}$, must be equal or exceed the sum of t_1 and t_3-t_2 , which are given by Eqs. 8 and 10, respectively, so that:

$$t_{3,min} > \frac{1}{\mu_{max}} \ln \left(\frac{\beta(1+\alpha)}{\alpha(1+\beta)}\right) + \frac{1}{\mu_{max}} \ln \left(\frac{\beta}{\alpha}\right)$$

or

$$t_{3,min} > \frac{1}{\mu_{max}} \ln \left(\frac{\beta}{\alpha} \right)^2 \left(\frac{1+\alpha}{1+\beta} \right) \quad \text{Eq. 13}$$

This can be conveniently evaluated with $t_{3,min}$ expressed as multiples of $\frac{1}{\mu_{max}}$ (see Fig. 2 in main manuscript). We see that the minimal duration of the pulse increases quasi-logarithmically with decreasing α , and that increasing β increases duration quasi-linearly. Also, that the minimal duration of the pulse becomes 0 only when $\alpha = \beta$, and that keeping α high for any given β , minimizes transition times.

6. Evaluation of net growth yield as a function of pulse duration

Equation 12 gives us the biomass attained during a pulse integrating the processes that occurred during growth and transition phases, G_3 , as a ratio to the initial biomass available G_0 and as a function the pulse's duration, t_3 , for a set of values of parameters α , β , and μ_{max} . Again here, it is convenient to evaluate the dependencies expressing time as multiples of $1/\mu_{max}$, which is related to the inherent maximal doubling time of the population, D , as $D = \ln(2)/\mu_{max}$.

A graphical evaluation of the effect of low, medium and high values of α , the portion of the biomass dedicated to reserves constitutively, with fixed β , and considering the minimal transition times derived in the previous section can be found in Fig. 3 of the main manuscript.

For low values of α , copious growth is attained only with long pulses whose duration exceed tens of times $1/\mu_{max}$, and the minimal transition period for success is above five times $1/\mu_{max}$. Conversely a high α results in moderate but positive growth for short pulses, even with pulses as short as $0.3/\mu_{max}$, but with low yields even for long pulses. Organisms with high α will outcompete those with low α if the pulses tend to be short, and vice-versa. This constitutes a biological adaptation strategy. Organisms that opt for low α can be called TOR and those that opt for high α , NIR.

One can also evaluate the influence of β , the portion of the biomass present as reserves at the beginning (and end) of the pulse. Fig. 3 in the main manuscript shows graphically the effects of varying β with fixed α . For very long pulses, beyond $100/\mu_{max}$ this has very little effect on yield. However, increasing β above unity increases the minimal length of the pulse to values well above $1/\mu_{max}$. Conversely, low β decreases this minimal threshold below $1/\mu_{max}$ at the expense of significantly lowered yield. Thus, organisms with low β will do better in short pulses. Within the range of medium sized pulses, around $10/\mu_{max}$, large β results in optimal yields. With very long pulses strategies of varying β become rather irrelevant.